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Individual Behavioral differences and health of golden-headed lion tamarins (*Leontopithecus chrysomelas*)

Running title: Behavior and health of *L. chrysomelas*

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ABSTRACT

Individual behavioral differences may influence how animals cope with altered environments and hence how these impact on their health status. We investigated the relationship between individual behavior of free-living golden-headed lion tamarins in one context (responding to a novel object) and their habitat use and health status (endoparasitism, clinical condition, fecal glucocorticoid metabolites). Four groups lived in landscapes with different levels of human disturbance: two in degraded forest fragments in agricultural matrix (DFAM), and two in cocoa agroforestry system (*cabruca*) in Atlantic Forest of South Bahia, Brazil. Using a subjective ratings approach, tamarins' responses to a novel object were classified according to a single

derived variable, 'confidence', with some individuals being 'high confident' ('bold', 'calm', low 'stressfulness' and 'fearfulness') and others 'low confident. Both response types occurred in both environments. 'High confident' individuals in DFAM landscapes spent less time foraging for animal prey than those in *cabruca*. Only DFAM individuals showed intestinal parasite infections, and their parasite loads were correlated with the number of grooming partners they had, suggesting an association between grooming and infection transfer. Glucocorticoid concentrations did not differ between animals from different landscapes. Individual Behavioral responses to novelty may thus be associated with tamarins foraging Behavior in human modified habitats, and social Behavior may be linked to the likelihood of parasitic infection. Individual Behavior in a test situation may thus have some predictive value for Behavior in a free-living context, and for its knock-on health consequences, but the causal direction of any links remains to be determined.

Keywords: conservation medicine, coping styles, parasites, primates, temperament.

1. INTRODUCTION

The Brazilian Atlantic Forest is ranked among the top biodiversity hotspots in the world, because of its species richness and extremely high levels of endemism (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). This biome, however, is also one of the most threatened on our planet due to habitat destruction and fragmentation (Colombo & Joly, 2010). There is relatively little information on how wild animals cope in fragmented habitats such as those of the Atlantic Forest, and how this impacts individual health and welfare (Acevedo-Whitehouse & Duffus, 2009; Delarue, Kerr, & Rymer, 2015; Zinsstag, Schelling,Waltner-Toews, & Tanner, 2011). Human-induced rapid environmental change (Sih, 2013) has imperilled many animal populations due to its effects on habitat fragmentation, climate change and environmental contamination (Deem, Karesh, & Weisman, 2001), which may lead to reduced food availability and impaired nutritional status (Amato et al., 2013). Animals that live in fragmented and degraded habitats usually face increased threats and challenges and may show higher faecal glucocorticoid metabolite levels than those living in more preserved areas (Balestri et al., 2014; Martinez-Mota, Valdespino, Sanchez-Ramos, & Serio-Silva, 2007). Prolonged elevation of glucocorticoid levels may negatively affect an animal's health (Acevedo-Whitehouse & Duffus, 2009; Breuner, Patterson, & Hahn, 2008; Cavigelli, 2005; Kumaresan, Palanisamy, Pasupuleti, & Arockiaraj, 2017). Whether individual Behavioral characteristics are associated with health (Capitanio, 2011) and survival in these changed environmental conditions has not been studied.

The relationship between individual personality/temperament and survival and fitness has been debated (Réale & Festa-Bianchet, 2003; Sih, Bell, & Johnson, 2004). Correlations between boldness and reproductive success have been found (Smith & Blumstein, 2008). Individuals who are more exploratory and take more risks may host higher parasite loads compared to ones with a lower propensity to explore and take risks (Barber, Mora, Payne, Weinersmith, & Sih, 2017; Bohn et al. 2017; Garcia-Longoria, Garamszegi, & Møller, 2014; Horváth et al., 2016; Patterson & Schulte-Hostedde, 2011). In contrast, shyer individuals expose themselves less to risky situations, by limiting their foraging activity in comparison with bolder ones (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), and this may adversely affect their nutritional status (Barber et al., 2017). The sociality of individuals can influence primates' general health (Capitanio, 2011). Non-human primates involved in more social interactions seem to have more health benefits than less social individuals do (baboons: Silk, Alberts, & Altmann, 2003; golden snub-nosed monkeys: Jin, Su, Tao, Guo, & Yu., 2013; rhesus macaques: Robinson et al., 2018). However, parasite flow due to variation in social interactions may also influence primates' health negatively (Rushmore, Bisanzio, & Gillespie, 2017). For instance, a study on parasite transmission in Japanese macaques (*Macaca fuscata yakui*) showed a clear bias in nematode prevalence toward high-ranking individuals, which occupy more central positions in both the outward and inward directed grooming networks (MacIntosh et al., 2012). Therefore, highly social individuals may be more susceptible to acquire parasites from other group-members (Barber & Dingemanse 2010; Godfrey, Bull, James, & Murray, 2009). Additionally, animals can vary in their neuroendocrine and Behavioral responses to acute stressors (Baugh et al., 2012; Koolhaas, Boer, Coppens, & Buwalda, 2010), which in turn may

influence their health, reproductive success, and survival (Breuner et al. 2008; Cavigelli, 2005). Consequently, individual Behavioral differences may be associated with health and wild population survival, which may have implications for conservation (McDougall, Réale, Sol, Reader, 2006; Smith & Blumstein 2008).

Studies of links between individual Behavior differences and health are of particular importance in endemic and threatened species such as the golden-headed lion tamarin (*Leontopithecus chrysomelas*) that are ecologically important but have a limited distribution range. The golden-headed lion tamarin is a small primate species of southern Bahia State in the Brazilian Atlantic forest (Pinto & Rylands, 1997). The species is classified as endangered (Kierulff, Rylands, Mendes, & Oliveira, 2008), due to forest loss resulting in degradation and fragmentation of its habitat (Kierulff et al. 2008). It interacts with up to 242 species of plants (Catenacci, De Vleeschouwer, Pessoa, & Nogueira-Filho, 2016a; Oliveira, Hankerson, Dietz, & Raboy, 2010) and plays an important role in Atlantic forest regeneration (Catenacci, De Vleeschouwer, & Nogueira-Filho, 2009). The animals live in social groups ranging from three to fifteen individuals (Oliveira, Neves, Raboy, & Dietz, 2011), usually composed of one dominant breeding pair, and a diverse number of offspring of various ages: adults, subadults, juveniles and infants (Rylands, 1993). Groups defend their territory against other lion tamarin groups using aggressive vocalizations such as long-calls, staccato of short whistles and chatter that can be also followed by agonistic interactions (Peres, 1989).

Most populations of tamarin live in unprotected areas altered by human activities, such as degraded forest fragments embedded in an agricultural matrix and *cabruca* – a shaded cocoa (*Theobroma cacao*) agroforestry system (Oliveira et al.,

2011; Raboy, Christman, & Dietz, 2004). Both of these environments (*agricultural matrix* and *cabruca*) present specific challenges to groups of tamarins, such as lower resource availability, higher exposure to predators, and higher hunting levels and human contact in comparison with groups living in more preserved areas (De Vleeschouwer & Oliveira, 2017; Oliveira & Dietz 2011; Raboy et al., 2004). These challenges may result in increased stress levels and affect the animals' health. Agricultural matrix composition and lack of connectivity may influence dispersal and persistence of primates (Anderson, Rowcliffe, & Cowlishaw, 2007). This environment, in general, seems to result in higher levels of disturbance and risks to animals, because non-forested patches of cultivated land, interspersed with roads, dirt paths and with frequent human presence typically characterize the agricultural matrix area (Anderson et al., 2007). In turn, *cabruca* is considered a valuable landscape because it connects forest patches, making populations less vulnerable to negative genetic effects of habitat fragmentation (Estrada, Raboy, & Oliveira, 2012). Furthermore, in contrast to other degraded landscapes, *cabruca* seems to provide important resources such as sleeping sites and bromeliads for foraging tamarins (Oliveira et al., 2011; Raboy et al., 2004). However, as far we know, no data concerning the links between tamarin individual Behavioral characteristics and health are available from either landscape.

In this study, we evaluated the relationship between individual Behavioral responses of tamarins in one context – exploration/avoidance of a novel object (Réale et al., 2007) – and individual health status in two different landscapes. We compared individuals from groups living in degraded forest fragments in an agricultural matrix, and in *cabruca* systems to determine whether the tamarins' Behavioral responses varied according to their environments (Wolf & Weissing, 2012). Furthermore, if exploratory

Behaviors and social interactions among individuals influence parasite flow (Barber & Dingemanse, 2010; Wren, Remis, Camp, & Gillespie, 2016), we predicted that more exploratory and more sociable individuals will show higher parasite loads compared to less exploratory and less sociable ones. Finally, as the agricultural matrix landscape poses a higher level of human disturbance compared to *cabruca*, and this is likely to be associated with greater stress and welfare challenges to tamarins, we also predicted lower levels of health and a higher incidence of raised fecal glucocorticoid metabolites concentrations, as an indicator of physiological stress, in the groups living in agricultural matrix.

2. METHODS

2.1. *Ethical note*

The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates and the Brazilian laws, where the present research was conducted. This work was approved by the Committee on Animal Research and Ethics of the Universidade Estadual de Santa Cruz, under protocol # 018/2015. The permission to capture, mark animals and collect biological materials was approved by the Brazilian Environmental Agency (ICMBio/SISBIO), under # 23457-6 and # 471783.

2.2. Animals and study areas

From August 2016 to April 2017 we studied 27 individuals (25 adults and 2 sub-adults (120DF and 121DF) (Table 1) belonging to four groups of golden-headed lion tamarins. Group composition changed over the study period, mainly due to births, predation, natural deaths or disappearances, and migration. Therefore, it was not possible to collect all types of data (novel object test, direct observation, sociality assessment, fecal sampling for glucocorticoid metabolites analysis, and parasite load) for all individuals. The information we collected for each individual in the four social groups is indicated in Table 1.

The tamarin groups lived in two landscapes of the Brazilian Atlantic forest in South-Bahia state. Two of these groups (RIB and MRO) lived in the rural area of the Municipality of Una (15°15'52"S, 39°8'46"W). This landscape is characterized by disturbed secondary forest patches in an agricultural matrix of pastures, rubber-trees, cassava, and cocoa crops, unpaved roads and intense human presence. We classified this area as 'degraded forest patches in agricultural matrix' – DFAM. The other two groups (ALM and BOM) lived at Almada and Bomfim private farms in the rural zone of Ilhéus, Bahia (14°39'S, 39°11'W), in a landscape characterized by the cocoa (*Theobroma cacao*) agroforestry system - *cabruca*. *Cabruca* is a system of shade cropping in which the middle and understory trees of intact forests are removed and replaced with cocoa trees but with preservation of the tall trees (Raboy et al., 2004). The two studied landscapes are part of the Atlantic Forest biome, characterized by high temperature and high relative humidity. In this region, temperature ranges from 19^0C to 28^0C, with an annual rainfall of over 2,100 mm (Coimbra-Filho & Mittermeier, 1973; Mori, Boom, Carvalho, & Santos, 1983).

The golden-headed lion tamarin groups from both landscapes, DFAM and *cabruca*, have been monitored and habituated to the presence of researchers since 2007 and 2014, respectively. Groups are monitored in the forest by using radio-telemetry and twice per year individuals are captured using banana bait and tomahawk traps (48.3 cm length × 15.2 cm width × 15.2 cm height), following procedures described in (Dietz, De Sousa, & Billerbeck, 1996). In the present study, after capture, we took the animals to a field laboratory (about 500m from the capture site), where they waited approximately four hours before being anesthetized (intramuscular 10 mg/kg ketamine and 0.3 mg/kg midazolam, following (Catenacci et al., 2016a). Anesthesia was applied by the first author, a veterinarian who checked the individuals' general clinical condition [heart rate (bpm), respiratory frequency (mpm) and temperature (ºC)] during sedation, determined the tamarins' sex and biometric measures [body mass (kg) and total length (mm)], and estimated their age. These procedures took around 20 minutes after sedation.

The individuals received a unique tattoo number and dye mark (Nyanzol Dye®) on the tail and arm, for identification during observations in the field. One or two individuals in each group were equipped with a radio collar (model RI-2D, Holohil Ltd., Ontario, Canada) to facilitate later monitoring and observation in the field using radio telemetry. In general, for this purpose, we chose the heaviest animals and always excluded pregnant females. We kept the subjects in the laboratory overnight to ensure full recovery from anesthesia and released them early in the morning of the next day at the site where they were captured. This procedure has been used and adapted to ensure animal safety over the course of the past 25 years, resulting in a very safe process with no detrimental effects on the animals if performed adequately (Catenacci et al., *in press*).

2.3. *Behavioral data collection*

For eight months (Aug 2016 - Jan 2017; Mar - Apr 2017), we followed each group for two days per month, resulting in a total of 506 hours of data collection. We used signals from the radio transmitter collars to locate each group before the animals woke up and observed them from the moment they left the sleeping site (tree hollow) in the morning until they entered the same or a different sleeping site in the evening. Each group was followed for about 22 hours a month. Individual marks disappeared in early January 2017 and forced us to suspend observations until the animals were captured again in March 2017, after which observations were resumed.

The golden-headed lion tamarins were observed using continuous focal animal sampling (Altmann, 1974); each focal observation lasted 10 min/animal. We randomized the order in which animals were observed, and when the last animal was observed, we restarted a new random order. When the animal disappeared from sight, the observation was interrupted and resumed when the animal was visible again. The observations were voice-recorded (digital voice recorder RR-US450 Panasonic, Ontario, Canada). Then, weekly in the lab, we calculated the proportions of observation time that each individual spent in social grooming and in the Behavioral categories related to exploration (eating, foraging for fruits and flowers or animal prey, and travelling). Behavioral states descriptions are provided in Table 2.

2.4. Individual Behavioral differences

Differences in the individual Behavior of tamarins were assessed using a test of exploration/avoidance of a novel object (Réale et al., 2007). Because gaining access to the individuals for testing was difficult, and hence it was not possible to measure individual Behavioral consistency over time in response to different types of challenge (Gosling, 2001; Sih et al., 2004), we evaluated individual tamarin Behavior in this context alone (Réale et al., 2007).

One week before the start of Behavioral data collection, we presented animals with a homemade flag (0.60 m length x 0.45 m height) of white fabric with five black dots (ø: 5.0 cm) on both sides of the flag. We set up the flag the day before the test and after animals had entered a tree hollow to sleep. The flag was set up in front of the entrance to the hollow, at a distance of 2.0m on average from the sleeping site.

During the novel object test, we video-recorded individual's response to the novel object when each one left the sleeping site and saw the flag for the first time, using a camcorder (DCR-SR45 Sony, Tokyo, Japan) for later video analysis. On most occasions, each individual left the tree hollow separately, but on two occasions (one in group ALM and another in group RIB) the next animal to leave put its head out of the tree hollow and watched the reaction of the previous one. Individual Behavior in the test analysis was assessed using a subjective rating approach validated for other species (cats: Feaver, Mendl, & Bateson, 1986; cattle: Sant'Anna & Paranhos da Costa, 2013; peccary: Nogueira, Macedo, Sant'Anna, Nogueira-Filho, & Paranhos da Costa, 2015) and adapted for golden-headed lion tamarins. The video clips (30 seconds) with each lion tamarin's reaction to the novel object were shown to three experts with experience in animal Behavior observations who had not participated in data collection (SSCN, SLGNF, and ASF). The judges were instructed to evaluate the animal's Behavior during

the flag test in terms of 14 adjectives providing descriptors of tamarin Behavioral style: 'relaxed', 'apathetic', 'calm', 'agitated', 'fearful', 'curious', 'stressed', 'alert', 'tense', 'active', 'shy', 'smart', 'bold', and 'cautious'. For each adjective (which was accompanied by a written definition (see Rouff, Sussman, & Strube, 2005), each judge placed a mark on a visual analogue scale represented by a line of 125 mm with a minimum value (0) at the left end of the line representing absence of the Behavioral characteristic and the maximum value (125) representing the most intense manifestation. The scores were obtained by measuring the distance in millimeters from the left end of the line to the judges' marks. The adjectives were previously chosen by primatologists' researchers (BR and DSF- who had not participated in data collection) based on studies of personality in nonhuman primates (*Macaca silenus*: Rouff et al., 2005; *Macaca nigra*, *Macaca sylvanus*, *Saimiri sciureus*: Baker, Lea, & Melfi, 2015), and on tamarin Behavioral repertoire.

2.5. Faecal samples collection and parasite analysis

While following groups for Behavioral data collection, we gathered fresh feces non-invasively from identified individuals immediately after defecation to determine both parasite load and fecal glucocorticoid metabolite concentrations. Feces were collected only during the morning until midday to minimize confounding effects of circadian rhythms on hormone levels. After collection, part of each sample was weighed and immediately preserved in 4% buffered formalin solution for later parasitological analysis (Monteiro et al. 2007). Sample weights ranged from approximately 0.5 to 1.5 g of feces. Parasite identification and parasite load (EPG:

number of eggs/g feces) were determined following a modified Ritchie's technique adopted by (Monteiro, Jansen, & Pinto, 2003; Monteiro et al. 2007) for golden lion tamarins (*Leontopithecus rosalia*). Nevertheless, due to the small amount of feces collected per individual, we could not test for fecal flotation (Willis method) (Gillespie, 2006). Part of this material was sent to Universidade Federal de Minas Gerais, Brazil for parasitological identification.

2.6. Faecal glucocorticoid metabolites concentration (FGCM) analysis

Part of each fecal sample, mentioned before, was used to assess the individual's glucocorticoid metabolite concentration. These samples were individually stored in Eppendorf plastic tubes labelled with individual identity, date and hour and kept inside Styrofoam at a mean temperature of 7°C until return to the field station in the evening after Behavioral data collection. Fecal samples were subsequently refrigerated (-20°C) at the field laboratory. On the following day, we took the fecal samples to Universidade Estadual de Santa Cruz where they were thawed to prepare for freeze-drying (FreeZone® Plus 4.5 l Cascade Benchtop, LABCONCO) following (Wasser et al., 2000).

The freeze-dried samples were sent to the Laboratory of Hormonal Measurements at the Federal University of Rio Grande do Norte, Brazil. In this laboratory an ELISA immunoassay for glucocorticoid metabolites, in which cortisol is the main hormone (around 60%), was performed in line with methods described by (Sousa & Ziegler, 1998). Accordingly, 0.1 g of feces was weighed, and steroids were extracted into 5 ml of ethanol at 50%. A 500 µl aliquot was reserved for solvolysis

(Ziegler et al., 1996) and after this procedure samples were resuspended in 500 µl of ethanol and stored at 5ºC until assay quantification.

The polyclonal anticortisol R4866 was used at dilution of 1:16.000 and the enzyme horseradish peroxidase conjugated to the antigen used at dilutions of 1:75.000. Both were obtained from University of California (Davis, CA, USA). The standard curves ranged from 3.16 to 1000 pg/ml. For assay precision assessment, intra- and inter-assay coefficients of variation (CV) were calculated. For intra-assay CV, the measured concentrations were used from samples run in duplicates in each assay, while inter-assay CV was estimated from concentrations of a high (30 % of binding) and low control (70 % of binding) run in each assay. Intra- and inter-assay CVs were 2.5 ± 1.3 % and 8.7 ± 3.0 %, respectively. For subsequent analysis, we used the individuals' glucocorticoid metabolites concentration mean obtained from each animal for which we had at least three samples collected in three different months over the study period.

2.7. Analysis of individuals' sociality

We used grooming interactions to assess the sociality of each individual in the tamarin groups. Through the observations, we identified the givers and receivers of grooming interactions and, using the software package SOCPROG 2.8 (Whitehead, 2009) we obtained the eigenvector centrality of each tamarin in the grooming interactions. The eigenvector centrality measures the importance of a node (that is, an individual) in a network. Individuals with high eigenvector centralities are connected to many other individuals that are, in turn, connected to many individuals (Whitehead, 2009). Following, we also used the software package SOCPROG 2.8 (Whitehead, 2009)

to obtain the network diagrams of social grooming for each group. From such network diagrams, we obtained the number of grooming partners of each individual allowing to test the correlation of this parameter with the parasite load following Wren et al. (2016).

2.8. Data analyses and statistics

To assess individual Behavioral characteristics during the novel object test (flag), we followed (Feaver et al., 1986) method. This method is based on non-parametric analysis, which is more appropriate method for small sample sizes ($N < 40$) (Feaver et al., 1986). In this analysis, seven golden-headed lion tamarins listed in Table 1 (13CF, 21CM, 23CM, 12CM, 120DF, 121DF, and 126DM) were not included because they were not present in the groups at the time of the test or we were unable to identify them during the novel object test. From the 14 adjectives used during subjective ratings (cited above), we used only those with Kendall's coefficients of concordance (W) > 0.70 among the three judges, as recommended by (Feaver et al., 1986). Six out of 14 adjectives (calm, agitated, fearful, stressed, shy, and bold, Table 3) showed $W > 0.70$ inter-judge concordance and were used to assess responses in the novel object test.

For each one of these most reliable six adjectives we calculated the mean value of the observers' ratings for each individual. Thereafter, to reduce the influence of distributional effects, the ratings of the three judges were converted to a z-score [(individual score - mean)/SD]. These mean z-scores were then checked for between-adjective correlations using Spearman rank correlation tests. Following that, highly correlated adjective descriptors were combined to produce z-score ratings, providing an indication of dimensions of Behavioral distinctiveness in exploration/avoidance of

golden-headed lion tamarins. One derived variable ('confidence') was selected to characterize responses in the novel object test.

To test our prediction of relationships between Behavioral characteristics with the landscape in which the animals live, we compared the proportion of time each tamarin was observed in the Behavioral categories related to exploration (eating, foraging for fruits and flowers or animal prey, and travelling) using mixed factorial ANOVA, considering landscape (*cabruca* x DFAM) and individual Behavior in the novel object test (high confident or low confident) as independent variables, followed by Tukey *post-hoc* tests when appropriate.

We used the same statistical model to compare the proportion of time each tamarin was observed in social grooming. As endoparasites were only recorded in fecal samples from golden-headed tamarins living in DFAM, we compared how parasite load of tamarins (EPG: eggs/g) varied according to individual's Behavioral characteristics using the *t*-test. Thereafter, we used Pearson correlation to test for a relationship between the number of grooming partners an individual had and its parasite load (EPG), followed by a linear regression analysis.

Subsequently, to test our prediction that the agricultural matrix landscape poses a higher level of human disturbance in contrast with *cabruca*, we compared the biometrical measures [body mass (kg) and total length (mm)], general health parameters recorded during sedation [heart rate (bpm); respiratory frequency (mpm), body temperature (°C)], and faecal glucocorticoid metabolites concentration (FGCM - ng/g dry faeces) between landscapes (*cabruca* x DFAM) using *t*-tests. Before the analyses, we evaluated if all data fulfilled the parametric requirements of normality of residuals and homogeneity of variance, and data were log transformed when necessary. Due to

lack of normality, we analyzed how the number of grooming partners were affected by sex (females vs. males) and landscapes (*cabruca* vs. DFAM) using non-parametric Mann-Whitney tests. The software Statistica 7.0 (StatSoft, Inc. 1984-2004) was used for all analyses, considering a $P < 0.05$ significance level.

3.0. RESULTS

3.1. Individual Behavioral differences in the novel object test

The six most reliable adjective descriptors of the Behavior of tamarins resulted in two groups of highly correlated ($r_s > 0.70$ or $r_s < -0.70$) variables (Table 4), which were combined in three Behavior categories named 'Explorer', 'Unperturbed', and 'Equable' in the following way:

(1) Explorer = (bold + not-fearful)/2

(2) Equable = (calm + bold)/2

(3) Unperturbed = (calm + not-stressed)/2

It should be mentioned that to properly combine the z-scores for each tamarin we determined the opposite z-scores of the following adjective descriptors: z-scores of not-fearful = (-1) * z-scores of fearful; z-scores of not-stressed = (-1) * z-scores of stressed. Moreover, there were correlations between explorer and equable rating z-scores ($r_s = -0.92$; $P < 0.0001$) and between explorer and unperturbed rating z-scores ($r_s = 0.69$; $P < 0.001$), and there was a correlation between equable and unperturbed rating z-scores ($r_s = 0.81$; $P < 0.0001$), meaning that these three adjective groups were all highly correlated and likely corresponded to just one Behavioral dimension, named

'confidence', which was used in further analyses. The four correlated ratings were combined in the following way:

(4) Confidence = (bold + calm+ not-fearful + not-stressed)/4

There were no differences in the mean (±standard deviation-SD) z-scores of the confidence Behavioral category for tamarins living in DFAM and *cabruca* (DFAM: 0.13 ± 0.99, $N = 9$, *cabruca*: -0.11 ± 0.73, $N = 11$, t-value = -0.63, $P = 0.54$). The mean (±SD) z-scores of the confidence Behavioral category also did not differ between female and male tamarins (Female: 0.01 ± 0.80, $N = 11$; Male: -0.01 ± 0.94, $N = 9$, t-value = -0.06, $P = 0.95$).

Eight individuals showed derived confidence scores which were above zero and hence were categorized as being 'high confident'. Of these animals, five lived in DFAM (92DF, 93DF, 82DM, 115DM, and 1DF) (Figure 1A) and three lived in *cabruca* (7CF, 14CM, and 9CF) (Figure 1B). Twelve individuals showed Behavior scores below zero and were categorized as being 'low confident'. Of these individuals, four lived in DFAM (125DF, 119DF, 118DM, and 102DM) (Figure 1A) and eight lived in *cabruca* (15CF, 5CM, 17CM, 18CF, 19CF, 20CF, 8CM, and 6CF) (Figure 1B).

3.2. Effects of landscapes and/or Behavioral category on time spent in Behavioral states, body parameters and parasite load

An interaction effect was detected between landscape type and Behavioral category ($F_{1, 13} = 7.76$, $P = 0.02$) on the proportion of time the tamarins spent on foraging for animal prey. The *post-hoc* test showed that high confident tamarins living

in *cabruca* landscapes spent a higher proportion of time on foraging for animal prey than the ones scored as high confident living in DFAM (Figure 2).

There were no effects of the landscape, Behavioral characteristics, or their interaction on the proportion of time that tamarins spent on travelling, foraging for fruits and flowers, and eating (Table 5). There were also no differences in biometrical measures, general health parameters, and glucorticoid metabolites concentration between tamarins living in cabruca and DFAM (Table 6). The complete information on each individual is presented in supplementary data (S1).

There were no parasite eggs in feces samples collected from golden-headed tamarins living in *cabruca*. In contrast, tamarins living in the DFAM were infected with four types of parasites: *Prosthenorchis* sp., *Trypanoxyuris* sp., *Primasubulura* sp., and Spiruridae. All parasites detected except *Prosthenorchis* sp., are nematodes. *Prosthenorchis* sp. is an Acanthocephala. In DFAM the parasite load (EPG: eggs/g) ranged from zero to 70.4 eggs/g of feces (S1), with a mean of 29.8 (SD = 19.6) eggs/g. There was no relationship between tamarins' Behavioral characteristics and parasite load (mean (± standard deviation) EPG high confident: 31.6 ± 24.7 eggs/g, $N = 5$; EPG low confident: 27.0 ± 31.8 eggs/g N = 4; t-value = 0.25, $P = 0.81$). The complete information on each individual is presented in supplementary data (S1).

3.3. Sociality and parasite load

There were no effects of Behavioral characteristics ($F_{1, 13} = 0.03$, $P = 0.87$), landscape ($F_{1, 13} = 0.94$, $P = 0.35$) or the interaction between Behavioral characteristics and landscape ($F_{1, 13} = 0.80$, $P = 0.40$) on the proportion of time tamarins spent in social

grooming. Social grooming was distributed unevenly among golden-headed tamarins. In general, male and female breeding individuals were involved in a higher grooming interaction rates (Figure 3) and showed higher eigenvector centrality indexes (supplementary data S1). For MRO group, the breeding female 1DF (eigenvector centrality: 0.68) was more involved in social grooming with the breeding male 102DM (eigenvector centrality: 0.63) (Figure 3A) than with other individuals of the group, whose eigenvector centrality ranged from 0.02 to 0.34 (Table 6). For RIB group, we identified two breeding females (92DF and 93DF). Female 92DF (eigenvector centrality: 0.65) was more involved in social grooming with the breeding male 82DM (eigenvector centrality: 0.65) than with the female 93DF (eigenvector centrality: 0.37) (Figure 3B) or other individuals of the group, whose eigenvector centrality ranged from 0.02 to 0.09 (supplementary data S1). For ALM group, we also identified two breeding females (18CF and 13CF). Female 18CF (eigenvector centrality: 0.52) was more involved in social grooming with the breeding male 23CM (eigenvector centrality: 0.62) than with the female 13CF (eigenvector centrality: 0.48) (Figure 3C) or other individuals of the group, whose eigenvector centrality ranged from 0.01 to 0.28 (supplementary data S1). In the BOM group (Figure 3D), the breeding female 20CF (eigenvector centrality: 0.70) was most involved in grooming interactions with the female 7CF (eigenvector centrality: 0.57) and with the male 8CM (eigenvector centrality: 0.25) (Figure 3D). It was not possible to confirm if male 8CM was the breeding male in this group because we did not record sexual interactions with the breeding female. The other two males of this group, however, showed lower eigenvector centrality in grooming interactions than the male 8CM (5CM and 12CM,

eigenvector centrality of 0.11 and 0.09, respectively). These results suggested that the male 8CM was the breeding male of the BOM group.

Overall, golden-headed tamarins had an average of 2.6 ±1.3 grooming partners (supplementary data S1). Females had similar numbers (mean ± standard deviation) of grooming partners (2.6 ± 1.4, $N = 15$) as males (2.6± 1.0, $N = 13$, $Z = 0.14$, $P = 0.89$). Moreover, tamarins living in *cabruca* had similar numbers of grooming partners (2.4 ± 1.1, $N = 16$) as the ones living in DFAM (2.8 ± 1.4, $N = 12$, Z = -0.66, $P = 0.54$). In DFAM, there was a correlation between the number of grooming partners that an individual had and its parasite load ($r_{Pearson} = 0.75$, $P = 0.01$, $N = 11$). This relationship followed the linear regression equation: EPG = 12.80 (number of grooming partners) - 10.50 ($R^2 = 0.57$, $F_{1, 9} = 11.83$, $P = 0.007$, $N = 11$, Figure 4).

4. DISCUSSION

As expected, free-living golden-headed lion tamarins showed individual differences in their reaction to a novel object test. Furthermore, 'high confident' individuals in this test who lived in the degraded forest fragments in agricultural matrix (DFAM) spent less time on substrate manipulation, foraging for animal prey, in comparison with 'high confident' ones living in *cabruca*. As we also expected, more sociable individuals showed higher parasite loads. In addition, we verified higher levels of parasite load for animals living in DFAM in comparison with those living in *cabruca*. Contrary to our predictions, however, there was no difference between fecal glucocorticoid metabolite concentrations in animals from these landscapes.

Responses to novelty in tests may indicate an individuals' propensity to explore or avoid a potential threat (Liebl & Martin 2012, Réale et al., 2007) and it was

interesting that high confident (more 'bold' and 'calm', whilst less 'fearful' and 'stressful') tamarins in DFAM spent less time on foraging for prey than high confident ones living in cabruca. Tamarins routinely show substrate manipulation searching for animal prey (Catenacci et al., 2016a, Raboy & Dietz, 2004), and we can only speculate as to the reason for this difference. One possible explanation is that DFAM animals had parasitic infections not observed in *cabruca* animals. The main infection symptoms of *Prosthenorchis* sp., the main parasite species found in DFAM, are loss of appetite, diarrhoea, and progressive weakness before death in the case of severe infections (Catenacci et al., 2016a). Thus, the *Prosthenorchis* sp. infection in DFAM animals may explain the relatively low amount of time spent foraging for animal prey recorded for high confident individuals in this landscape. In addition, the most infected animals in DFAM were the breeding individuals, who performed more grooming as well.

It has been suggested that high levels of sociality are usually associated with good animal health (Capitanio, 2011; Jin et al., 2013; Robinson et al., 2018). Social grooming, for instance, is important for removal of ectoparasites, maintenance of social bonds and/or to reduce social tension in groups of non-human primates (Dunbar, 1991; Lehmann, Korstjens, & Dunbar, 2007). Indeed, in our study we observed that breeding female and male of the groups showed more grooming interactions with each other, probably to reinforce their pair bond. In addition, our data suggests that the individual's eigenvector centrality may be used to identify the putative breeding male in golden-headed tamarin groups when there is no record of sexual interactions, although this needs to be confirmed in further studies.

Social grooming, however, can increase the risk of transmission of parasites due to direct contact with infected individuals and ingestion of ecto- and endoparasites

(Drew, 2010; Gillespie, 2006; MacIntosh et al., 2012). In agreement with this, we found a positive association between the number of grooming partners and parasite load for animals from DFAM. We speculate that fecal contamination of fur and skin may occur in golden-headed tamarins. If so, the groomer may ingest some larvae during grooming, as suggested for wild vervet monkeys (*Chlorocebus aethiops*), a species in which a positive correlation between the number of grooming partners and intestinal parasites infection was also observed (Wren et al., 2016). The same was recorded for Japanese macaques, with individuals who occupied more central positions in grooming networks exhibiting more infection by nematodes (MacIntosh et al., 2012). Our study, together with other findings (MacIntosh et al., 2012; Wren et al., 2016) shows the importance of investigating social bonds among individuals to provide information about the direction of endoparasite transmission. Parasite contamination of tamarin group members might also occur during sharing of the sleeping site (tree hollow). However, we might have then expected a more even distribution of parasites, but we observed more social animals to have a greater parasite infection. Thus, although it is possible that parasite contamination occurred during sleep time, grooming Behavior may have been an important contamination mechanism.

Our prediction that tamarins in DFAM have poorer health was supported by the observation of higher parasite load in the DFAM compared to the *cabruca*. In our study, the principal parasite that infested animals from DFAM was *Prosthenorchis* sp., an acanthocephalan helminthic. This parasite has a complex life cycle, having invertebrates as intermediate hosts, and vertebrates as final hosts (Machado-Filho, 1950). The transmission between tamarins possibly occurred by sharing contaminated food (invertebrates), a typical Behavior observed for this species (Moura, Nunes, &

Langguth, 2010), or sites of food found in bromeliads, increasing chances of infection among more sociable individuals. *Prosthenorchis* sp. infection is associated with apathy, inappetence and gastrointestinal symptoms; and may cause high mortality in primates (Catenacci et al. 2016b, Pissinatti, Pissinatti, Burity, Mattos Jr, & Tortelly, 2007). This information raises questions on how tamarins are coping with altered environments and how this high level of infection affects individual health, reproduction, and ultimately individual and species survival. Moreover, we do not know how different levels of disturbance may affect tamarin health and welfare. Therefore, more investigation is needed to understand the causes of the abundant presence of *Prosthenorchis* sp. and its relationship with tamarins in DFAM. In turn, the absence of *Prosthenorchis* sp. in *cabruca* may be explained by the use of pesticides in this plantation system which may disturb insect populations (Delabie, 1990), which are the intermediate hosts of *Prosthenorchis* sp. (e.g. Blattodea and Coleoptera; (Stunkard, 1965), and part of the tamarins' diet (Catenacci et al. 2016a). Thus, the decreased density of insects in *cabruca* probably avoids and/or reduces the chances of tamarin contamination.

Other factors, such as stress and inferior nutritional condition in fragmented environments can affect host susceptibility to parasites (Santicchia et al., 2015). However, the basal faecal glucocorticoid metabolites concentration (FGCM) did not differ between the studied landscapes. Moreover, the FGCM levels were within normal ranges shown for the genus *Leontopithecus* sp. (Wark et al. 2016). This result is unexpected, because DFAM landscape supposedly presents a more challenging environment for the animals due to anthropogenic impacts such as deforestation for agricultural proposes and opening of roads, compared to *cabruca*. On the other hand,

tamarins are exposed to high levels of natural predation risk in *cabruca* (Oliveira & Dietz, 2011), which represent another ecological challenge.

Usually, animals facing environmental stressors such as high levels of predation, food scarcity or anthropogenic disturbance as we observed in both landscapes have higher glucocorticoid levels (Busch & Hayward, 2009; Rangel-Negrín, Alfaro, Valdez, Romano, & Serio-Silva, 2009). In a study with howler monkeys (*Alouatta pigra*) living in fragmented forest, for instance, glucocorticoid levels were higher compared to animals living in continuous forest (Martinez-Mota et al., 2007). In general, food scarcity is an important factor responsible for poor welfare and increase of glucocorticoids in the wild (sifakas (*Propithecus diadema*), Irwin, 2007; wild black capuchins (*Sapajus nigritus),* Moreira, Santos, Sousa, & Izar, 2016). However, food availability seems not to be a great challenge for tamarins as the proportion of time spent in foraging and eating fruits were similar in both landscapes. This might be because this species can eat several fruit species available in fragmented forest (Catenacci et al., 2016a). Stress hormone levels may reflect current levels of disturbance (Beehner & Bergman, 2017) but their links with long-term fitness are much less clear (Busch & Hayward, 2009). Glucocorticoid metabolite data should thus be interpreted carefully (Dawkins, Edmond, Lord, Solomon, & Bain, 2004; Nogueira, Calazans, Costa, Peregrino, & Nogueira-Filho, 2011) and alongside other indicators of animal welfare such as the Behavioral and health indicators measured here.

There is little information on health parameters of tamarins and because of this, the health and physiological data collected here were compared with reports for the genus *Leontopithecus*. Comparisons indicated that the respiratory frequency, heart rate, and body temperature of tamarins recorded under anaesthesia in both landscapes were

within normal range for the genus (Verona & Pissinatti, 2014). Overall, the clinical examination and health parameters evaluated in our study suggest that tamarins were within acceptable health parameters despite the parasite infections and the environmental challenges found in DFAM.

Overall our results point to associations between individual differences in Behavior in test situations, and Behavior under free-living conditions, and between social structure and parasite transmission. Whilst the precise reasons for these associations, and their causal direction, cannot be determined from the current data, further research may indicate whether they support the notion that social Behavior plays an important role in ecological and evolutionary processes (Smith & Blumstein, 2008; Wolf & Weissing, 2012). If so, a better understanding of individual differences may have implications for conservation strategies of the golden-headed lion tamarin, such as forest restoration aiming to regain ecological integrity and enhance tamarin's welfare in a challenging environment – the Brazilian Atlantic forest.

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939 Tables and Tables legends

940

941 Table 1. Characterization of golden-headed lion tamarins' individuals of each

942 group and description of data collected.

Individual	Group	Landscape	Sex	Weight (kg)	Length (mm)	Evaluation ‡	Obs.
14CM	ALM	CAB	M	0.69	633	1,2,3, 4,5	
15CF	ALM	CAB	F	0.60	640	1,2,3,4,5	
17CM	ALM	CAB	M	0.68	621	1,2,3,4,5	
18CF	ALM	CAB	F	0.53	652	1,2,3,4,5	Breed. Fem.
19CF	ALM	CAB	F	0.69	623	1,2,3,4,5	
13CF	ALM	CAB	F	0.64	625	3	Breed. Fem.
21CM	ALM	CAB	M	0.57	615	3	
23CM	ALM	CAB	M	0.68	629	3	Breed. Male
5CM	BOM	CAB	M	0.63	645	1,2,3,4,5	
6CF	BOM	CAB	F	0.73	663	1,2,3,4,5	
7CF	BOM	CAB	F	0.68	663	1,2,3,4,5	
8CM	BOM	CAB	M	0.57	623	1,2,3, 4,5	
9CF	BOM	CAB	F	0.64	605	1,2,3,4,5	
12CM	BOM	CAB	M	0.51	624	3	
20CF	BOM	CAB	F	0.62	580	1,2,3,4,5	Breed. Fem.
82DM	RIB	DFAM	M	0.65	610	1,2,3,4,5	Breed. Male
92DF	RIB	DFAM	F	0.69	590	1,2,3,4,5	Breed. Fem.
93DF	RIB	DFAM	F	0.65	605	1,2,3,4,5	Breed. Fem.
118DM	RIB	DFAM	M	0.61	607	1,2,3,4,5	
119DF	RIB	DFAM	F	†	†	1,2,3,4,5	
126DM	RIB	DFAM	M	0.58	615	3	
102DM	MRO	DFAM	M	0.58	690	1,2,3,4,5	Breed. Male
115DM	MRO	DFAM	M	0.63	636	1,2,3,4,5	

120DF	MRO	DFAM	F	0.48	565	3	Sub-adult
121DF	MRO	DFAM	F	0.43	586	3	Sub-adult
125DF	MRO	DFAM	F	0.61	630	1,2,3,4,5	
1DF	MRO	DFAM	F	†	†	1,2,3,4,5	Breed. Fem.

Symbols code: Individual: number followed by landscape (C: *cabruca* and D: DFAM) and sex (F: female and M: male); Group: ALM: Almada; BOM: Bomfim; RIB: Ribeiro; MRO: Manoel Rosa; Landscapes: CAB: *cabruca*; DFAM: degraded forest fragments in agricultural matrix; Sex: M: male; F: female. Evaluations: 1 = novel object test; 2: Behavioral direct observation; 3: sociality assessment; 4: parasitological analysis; 5: faecal glucocorticoid metabolite concentrations. Breed. Fem.: breeding female; Breed. Male: breeding male.

†Data not available; ‡ Evaluation: indicates the test or measure in which each individual participated.

Table 2. Behavioral states recorded by direct observation of golden-headed lion tamarins.

Behavior	Definition
†Social grooming	The individual gives or receives grooming Behavior – manipulation of the fur of another conspecific with hands or mouth.
‡Eating	The individual manipulates or puts inside its mouth fruits, flowers, nectar, gum or animal prey.
‡Foraging for fruits and flowers	The individual appears to be visually searching for fruits and flowers.
‡Foraging for animal prey	The individual uses manipulative foraging to locate animal prey concealed in sites such as dried leaves and tree bark.
‡Travelling	The individual is moving from one place to another, covering a certain distance.

†Adapted from (Muroyama, 1991). ‡Adapted from (Raboy & Dietz, 2004).

Table 3. Inter-observer Kendall's concordance coefficients (*W*) of ratings of free-living golden-headed lion tamarins' Behaviors.

Adjective	W	*P*
Active	0.55	<0.05
Agitated	**0.84**	<0.05
Alert	0.63	<0.05
Apathetic	0.54	<0.05
Bold	**0.80**	<0.05
Calm	**0.92**	<0.05
Cautious	0.61	<0.05
Curious	0.64	<0.05
Fearful	**0.80**	<0.05
Relaxed	0.60	<0.05
Shy	**0.81**	<0.05
Smart	0.40	<0.05
Stressed	**0.76**	<0.05
Tense	0.66	<0.05

Items in bold type are those in which the inter-observer Kendall's concordance coefficients (*W*) were greater than 0.70 and thereby qualified for use in further analysis.

Table 4. Spearman correlations coefficients of mean ratings of descriptor adjectives.

	Calm	Agitated	Fearful	Stressed	Alert	Bold
Calm	-					
Agitated	0.36	-				
Fearful	-0.58	-0.13	-			
Stressed	**-0.71**	-0.22	0.51	-		
Alert	-0.45	-0.57	0.41	0.11	-	
Bold	**0.71**	-0.01	**-0.72**	-0.56	-0.19	-

Bold values represent $r_s > 0.70$ or $r_s < -0.70$ used to combine the Behavioral descriptors.

Table 5. *F* (and *P* values) of mixed factorial ANOVA performed to compare proportions of time tamarins spent on travelling, foraging, and eating Behavioral categories, considering landscape (*cabruca* x DFAM) and individual Behavior in the novel object test (high confident and low confident) as independent variables.

Behavioral categories	Landscape	Behavioral characteristics	Interaction†
Travelling	1.21 ($P = 0.29$)	0.30 ($P = 0.59$)	0.19 ($P = 0.67$)
Foraging‡	1.43 ($P = 0.25$)	0.15 ($P = 0.70$)	0.05 ($P = 0.83$)
Eating	2.63 ($P = 0.13$)	0.47 ($P = 0.50$)	0.12 ($P = 0.73$)

†Interaction between landscape and Behavioral characteristics.

‡Foraging for fruits and flowers.

Table 6. Means and standard deviation (SD) of biometrical measures, general health parameters during sedation, and faecal glucocorticoid metabolite concentrations (FGCM - ng/g dry faeces) of golden-headed lion tamarins (*Leontopithecus chrysomelas*) living in *cabruca* (cocoa agro-forestry) and degraded forest patches in agricultural matrix (DFAM) landscapes.

Item	*Cabruca* (*X*)	SD	*N*	DFAM Mean	SD	*N*	*t*-test	*P*
Morphological measures								
Body mass (g)	644	72	9	637	34	8	-0.28	0.78
Total length (mm)	629	27	9	622	31	8	-0.50	0.62
General health parameters								
Heart rate (bpm)	244	14	9	240	47	8	-0.24	0.81
Respiratory frequency (mpm)	38	9	9	44	12	8	1.01	0.33
Body temperature (°C)	37	0.6	9	37	0.5	8	1.15	0.27
FGCM (ng/g dry faeces)	947	442	9	1141	240	8	1.10	0.29

S1. Overview of results from parasitological analysis, parasite load (EPG eggs/g), physiological parameters and fecal glucocorticoid metabolites concentration mean (FGCM ng/g) and eigenvector centrality in grooming interactions of golden-headed lion tamarins (*Leontopithecus chrysomelas*) living in *cabruca* (CAB) and degraded forest patches in agricultural matrix (DFAM) landscapes.

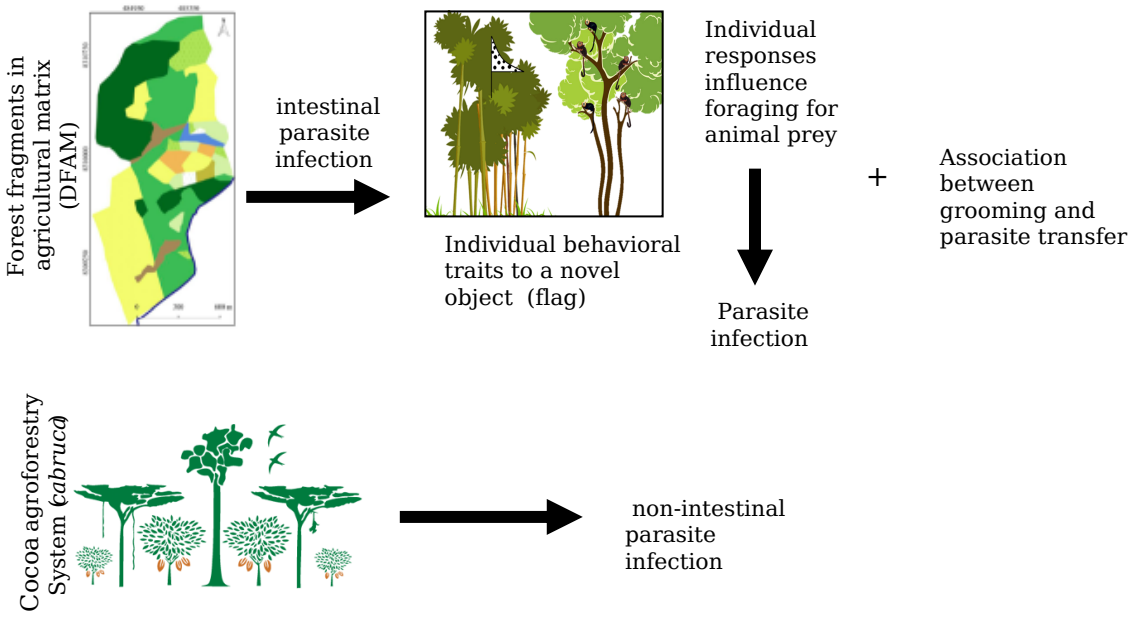
Animal	Group	Landscape	Sex	Parasite Identification	EPG mean	Heart rate (bpm)	Respiratory frequency (mpm)	T(°C)	FGCM mean	Eigenvector centrality
14CM	ALM	CAB	M	not present	0.00	240	32	36.4	1522.78	0.17
15CF	ALM	CAB	F	not present	0.00	180	20	34.8	1383.67	0.01
17CM	ALM	CAB	M	not present	0.00	240	60	36.8	118.86	0.28
18CF	ALM	CAB	F	not present	0.00	264	28	36.4	1022.85	0.52
19CF	ALM	CAB	F	not present	0.00	260	40	37.5	1155.71	0.04
5CM	BOM	CAB	M	not present	0.00	228	36	35.3	†	0.11
6CF	BOM	CAB	F	not present	0.00	248	44	37.0	776.67	0.32
7CF	BOM	CAB	F	not present	0.00	248	44	38.0	1382.88	0.57
8CM	BOM	CAB	M	not present	0.00	240	36	37.0	631.46	0.25
9CF	BOM	CAB	F	not present	0.00	240	32	37.5	654.42	0.08
20CF	BOM	CAB	F	not present	0.00	216	32	35.8	1258.13	0.70

82DM	RIB	DFAM	M	*Prosthenorchis* sp.	8.59	240	32	36.3	926.38	0.65
92DF	RIB	DFAM	F	*Prosthenorchis* sp.	10.59	252	44	37.1	1331.1	0.65
93DF	RIB	DFAM	F	*Prosthenorchis* sp. and *Trypanoxyuris* sp.	63.89	292	60	37.4	1129.28	0.37
118DM	RIB	DFAM	M	*Prosthenorchis* sp., *Primasubulura* sp. and Spiruridae	70.42	304	60	37.8	1500.09	0.09
119DF	MRO	DFAM	F	*Prosthenorchis* sp.	31.14	†	†	†	589.757	0.04
102DM	MRO	DFAM	M	*Prosthenorchis* sp.	3.27	160	44	37.1	1205.52	0.63
115DM	MRO	DFAM	M	*Prosthenorchis* sp.	24.05	200	48	37.0	858.727	0.11
125DF	MRO	DFAM	F	*Prosthenorchis* sp.	6.68	218	23	38.0	861.13	0.34
1SF	MRO	DFAM	F	*Prosthenorchis* sp.	51.02	*	*	*	1321.18	0.68

†Data not available. ALM: Almada, BOM: Bomfim, RIB: Ribeiro, MRO: Manoel Rosa, EPG = parasite load (eggs/g); FGCM=Fecal glucocorticoid metabolites concentration; T(°C) = body temperature

Research Highlights

- Individual Behavioral responses to novelty were correlated with foraging for animal prey.
- Only individuals from degraded area showed intestinal parasite infections.
- The parasite loads were correlated with the number of grooming partners.



Graphical abstract. Only DFAM individuals showed intestinal parasite infections, and their parasite loads were correlated with the number of grooming partners they had, suggesting an association between grooming and infection transfer. High confident' individuals in DFAM landscapes spent less time foraging for animal prey than those in *cabruca*

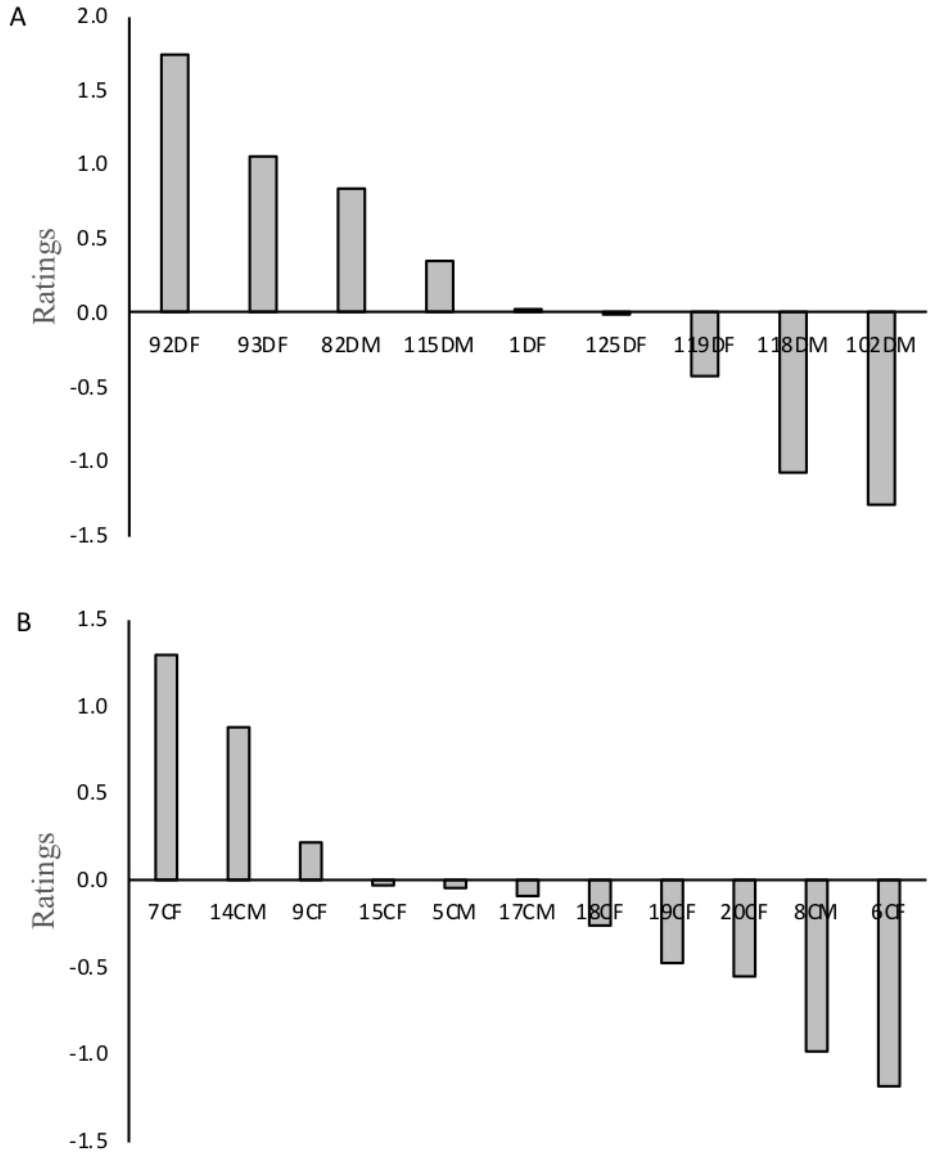


Figure 1. Behavioral ratings of tamarins from DFAM (A) and cabruca (B) on the confidence Behavioral dimension. The ratings for confidence dimension were obtained from the z-scores (bold + calm+ not-fearful + not-stressed)/4. The numbers identify the individual tamarin, the letters D and C the landscapes (D: DFAM, C: cabruca) and M and F correspond to animal's sex (M: male, F: female).

199x247mm (96 x 96 DPI)

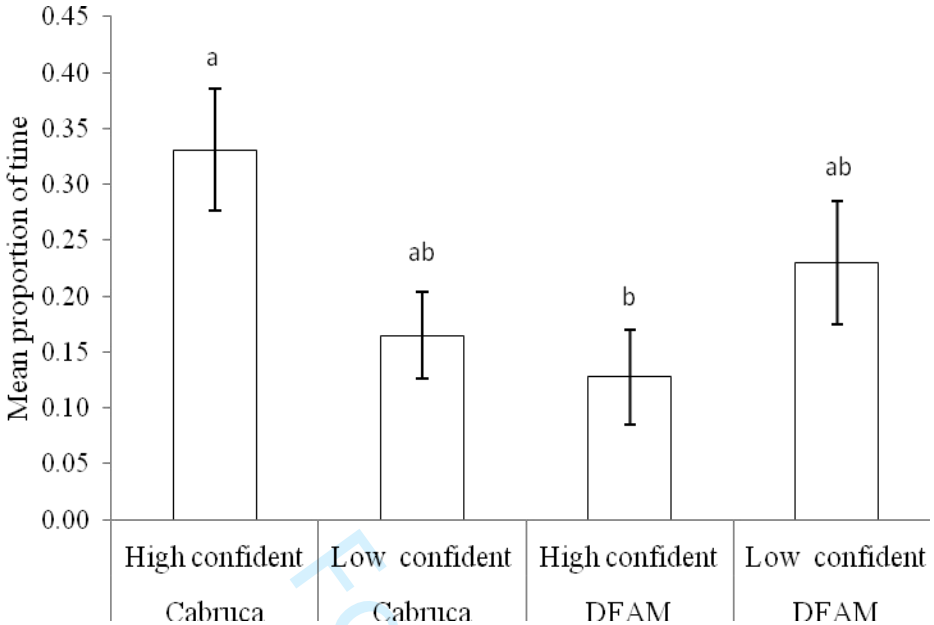


Figure 2. Means proportion of time golden-headed lion tamarins spent in foraging for animal prey according their behavioural category (high confident and low confident) and area (DFAM: degraded forest patches in agricultural matrix; *cabruca*: cocoa agro-forestry). Error bars show standard errors and columns with different letters are significantly different ($P < 0.05$, Tukey *post-hoc* tests).

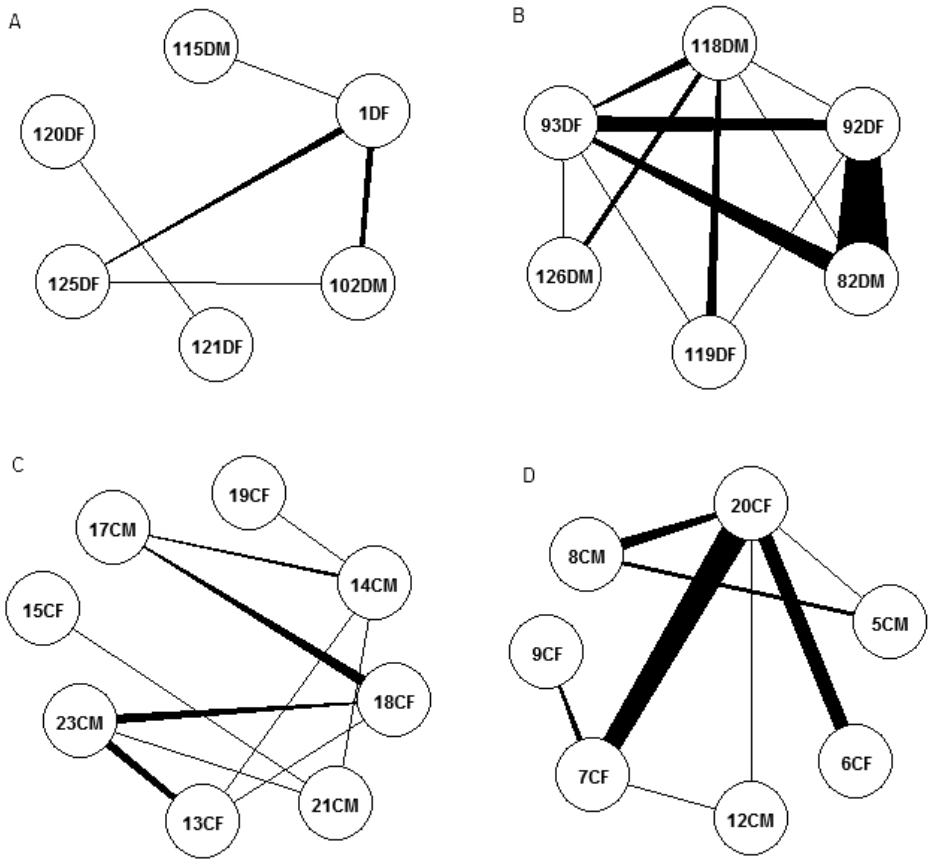


Figure 3. Network diagrams of the grooming interactions among golden-headed lion tamarins' groups (A: Manoel Rosa, B: Ribeiro, C: Almada, D: Bomfim). The alphanumeric code inside the boxes identified the individuals: their number, landscape (C: cabruca or D: DFAM), and sex (M: male or F: female). The arrows point the provider/recipient of the interaction and its thickness indicates the strength of the interaction rate between individuals.

176x158mm (96 x 96 DPI)

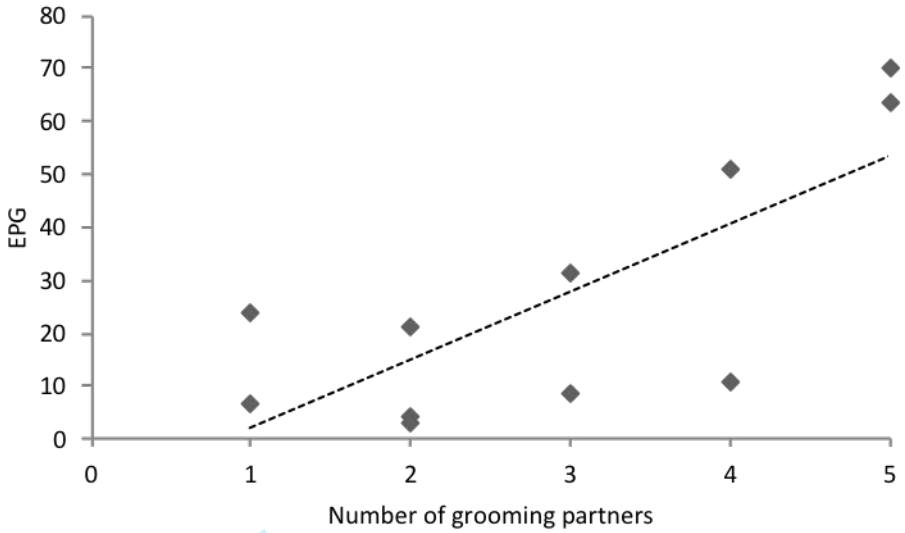


Figure 4. Relation between number of grooming partners and EPG (number of eggs/g faces) in golden-headed tamarins in agricultural matrix (DFAM) landscape following the linear equation EPG = 12.80 (number of grooming partners) - 10.50 (R^2 =0.57, $F_{1, 9}$ = 11.83, P = 0.007, N = 11).

S1. Overview of results from parasitological analysis, parasite load (EPG eggs/g), physiological parameters and fecal glucocorticoid metabolites concentration mean (FGCM ng/g) and eigenvector centrality in grooming interactions of golden-headed lion tamarins (*Leontopithecus chrysomelas*) living in *cabruca* (CAB) and degraded forest patches in agricultural matrix (DFAM) landscapes.